

MIGRATORY RESTLESSNESS IN CAGED BOBOLINKS  
(*DOLICHONYX ORYZIVORUS*, A TRANS-  
EQUATORIAL MIGRANT)<sup>1</sup>

WILLIAM L. ENGELS

*Department of Zoology, University of North Carolina, Chapel Hill, N. C.*

It has been known for a very long time that caged migratory birds become increasingly restless at the onset of the migratory season. This restlessness is expressed especially by fluttering and hopping on the perches after dark when, ordinarily, caged birds sit quietly. Most investigators have assumed, at least tacitly, that the development of such nocturnal restlessness reflects the development of a disposition to migrate. It is frequently referred to as *Zugunruhe* (migratory unrest). Thus equated with migratory behavior, it could be a useful indicator in various aspects of the experimental study of migration (*e.g.*, regulation, physiology, navigation).

In the past three decades there have been a number of studies on the induction and regulation of this restlessness with respect to such factors as temperature, food, sex hormones, and photoperiod. Although one may doubt in some cases that the restlessness truly reflected a migratory state, there is clear evidence for the photoperiodic induction of migratory behavior in at least a few temperate zone migrants (*e.g.*, King, 1961, *Zonotrichia leucophrys gambelii*). Transequatorial migrants have received little attention although obviously they are of special interest in relation to photoperiodism. Each of their two annual migrations, northward and southward, begins during the declining day-lengths of late summer or early autumn in one hemisphere and ends during the increasingly longer days of middle or late spring in the other. In his studies on star-navigation by birds Sauer (1957) has employed restlessness in the European-African transequatorial migrant *Sylvia borin* to determine directional orientation. Recently Hamilton (1962) demonstrated orientation under clear skies in the nocturnal restlessness of caged bobolinks during both spring and fall migratory periods. Neither of these was concerned with the induction or regulation of the restlessness *per se*, although an intrinsic rhythm seems to be implied for *S. borin* (Sauer and Sauer, 1955).

It has already been shown that the annual testicular cycle of caged bobolinks (*Dolichonyx oryzivorus*) is under photoperiodic control (Engels, 1959, 1961). This species breeds in North America above Lat. 40° N., reaching the nesting area in late May or very early June after a migration, begun in late March or early April, from a "wintering" area in South America lying roughly between Lat. 10° and 30° S. It is then of some interest to determine if caged bobolinks display a seasonal nocturnal restlessness which may be related to migratory behavior and controlled or influenced in any way by day-length.

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## MATERIALS AND METHODS

The bobolinks used in these experiments were captured in North Carolina at about Lat. 36° N., some in May, others in September, thus near the end of the northward or shortly after the beginning of the southward migration. These are referred to hereafter as "spring captures" and "autumn captures," respectively. Some individuals were used as experimental animals in successive years; after the first year these are designated "2nd year experimentals." Each such bird had spent at least six months (June through November) in an outdoor aviary exposed to natural day-lengths before being used in another experiment.

Over a three-year period four groups of birds were used, confined in outdoor aviaries exposed to normal outside air temperatures. Of these, two groups experienced only natural day-lengths (Lat. 36° N.), while two were exposed to constant 14-hour photoperiods beginning in November. The birds were confined individually in small cages placed on a shelf in the sheltered rear part of the otherwise open aviaries.

The cages used were "Hendryx finch-breeder" cages measuring about 8 × 9 × 16 inches. Each was fitted with two perches which pivoted at one end on a horizontal metal rod ( $\frac{1}{8}$  inch diameter) placed about three inches outside the rear of the cage and attached to it at each end by a frame. At the front each perch rested on a microswitch attached to the cage. Closure of either switch, resulting from a depression of the perch as the bird hopped on it, actuated an electronic counting device,<sup>2</sup> each closure advancing a four-digit counter by one. Every 15 minutes the accumulated count automatically was printed on a clock-motor-driven, chronologically marked tape, and the counter then returned to zero.

To each cage were attached a food-hopper and two 100-cc. water tubes which provided at one filling sufficient food and water to supply a bobolink of normal behavior for more than a week. A small amount of soluble terramycin was added to the drinking water. At first a chick laying-mash (Purina Layena) was used as food; we later changed to a mash prepared for game birds (also Purina). The pan of the cage was covered with a layer of finely crushed granite.

The birds were left undisturbed except for periodic handling for weighing and inspection of the plumage. This was done usually once a week. On these occasions the cages and water tubes were cleaned, fresh water and clean granite supplied and the food-hopper refilled. Body weight was determined on a balance reading to the nearest 0.01 gram and recorded to the nearest 0.1 gram.

An enormous amount of raw data on perch hopping activity was accumulated over the three seasons of observation. To reduce this to manageable and meaningful figures, three indices were used, as follows:

*Index A:* This is simply the number of quarter-hour periods during the night in which one or more perch movements were recorded. (This is similar to the index used by Weise, 1956, but his interval was a more satisfactory 0.1 hour). Such periods may be designated as *active night periods*. Selection of the quarter-hour as the basic interval was dictated by the recording device, which automatically printed out the number of perch movements every 15 minutes. *Night* here means the total dark period for birds exposed to artificial illumination, or, for birds exposed to natural photoperiods, the interval between the end of evening civil

<sup>2</sup> "Tally-Print," Model AR, Standard Instrument Corp., New York.

twilight and the beginning of morning civil twilight. Obviously, one hop per quarter-hour is hardly indicative of restlessness, but the index has usefulness and value when combined with the next index (B), as giving some information on the possible maximum duration of unrest during the night.

*Index B:* This is the average number of perch movements (hops) recorded per active night period and thus is an expansion of Index A.

*Index C:* This is the total number of perch movements (hops) recorded during the night, the product of the first two indices.

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## RESULTS

### *Experiment 1 (Table I)*

During the fall, winter and spring of 1959-60, essentially continuous records of perch-hopping activity were obtained for four males confined in an outdoor aviary and thus exposed to essentially natural day-lengths and normal air temperatures.

TABLE I

*Summary of nocturnal activity of four male bobolinks in relation to season, natural photo-period, and ambient temperature, as measured by recorded perch-hopping movements, January 3 to May 3, 1960, Chapel Hill, N. C., Lat. 36° N. Outdoor aviary, natural lighting only*

Week ending	Air T ° C.		Nocturnal Activity Indices		
	Aver. H	Aver. L	A	B	C
Jan. 10	9	-1	1.4	3.0	4
17	18	+4	9.9	21.2	210
24	6	-6	2.2	7.6	17
31	11	-1	6.0	5.9	35
Feb. 7	11	-1	6.5	13.1	85
14	13	-1	1.9	3.8	7
21	8	-4	<1	1.5	<1
28	9	-3	1.2	5.0	6
Mar. 6	4	-6	<1	5.0	<1
13	2	-8	<1	2.5	<1
20	7	-2	3.0	19.4	58
27	12	-3	17.6	41.4	729
Apr. 3	23	+9	17.3	79.0	1367
9	21	7	25.7	54.2	1393
19	23	8		<i>no records</i>	
26	28	12	22.8	66.6	1518
May 3	23	8	24.9	86.1	2144

Nocturnal Activity Index A: average number of active quarter-hour periods per bird per night (one or more hops recorded during the quarter-hour period); B: average number of hops recorded per active quarter-hour night period; C: average number of hops per bird per night. See text.

The photoperiod (including twilight) increased from a low of about 10½ hours in December to about 15 hours in May. Two of the four males were "autumn captures," one was a "spring capture" and one a "2nd year experimental." The latter two both had experienced natural day-lengths through the summer of 1959. (These are the birds designated as "Group F" in Engels, 1961, Table II, p. 143.)

Through the autumn these birds displayed bursts of nocturnal activity in a somewhat sporadic manner, but this eventually declined in intensity, more or less coincident with the advent of cold weather. At this time diurnal activity also declined, so that frequently an individual bird did not record more than 100 perch movements in a 24-hour period. The nocturnal activity indices for these birds, from January 4 to May 4, are presented as weekly averages in Table I, together with average high and low air temperatures as recorded by the local station of the U. S. Weather Bureau. It will be noticed that all indices have low values from January on through the week ending March 20. The slight elevation of the indices for the week ending January 17 might be a reflection of the slight rise, about 6° C., in average ambient temperature. However, the sharp rise in all indices apparent for the week ending March 27 occurred while the average low (night) air temperatures were still below the freezing point. Although the continued maintenance of intensive perch-hopping activity during the nights of succeeding weeks coincided with the normal spring rise in air temperature, the whole picture does suggest a nocturnal restlessness induced by something other than an increase in environmental temperature.

The intensification of nocturnal activity was also more or less coincident with a photoperiodically induced production of male sex hormone. This latter event is manifested in bobolinks by a change in the pigmentation of the horny beak, which eventually becomes a deep glossy black (Engels, 1959, p. 761). With one exception the onset of nocturnal restlessness was abrupt, occurring in a single night. The actual dates for the individual birds were the nights of March 19/20, 23/24 and April 5/6. For one bird restlessness began also on March 23/24, then slacked off after a few nights but was persistent every night after April 3/4. In two cases this onset of restlessness preceded the initial appearance of beak pigmentation by at least a week, in one case by at least three days, and in the fourth bird the two events may have been essentially coincident.

Two of the four birds went through an almost complete prenuptial molt. In both, molting was intense and general in early February and continued on into mid-March. During this period body weight diminished by about 10 grams or by about 20 to 25%. In both, nocturnal restlessness appeared within one or two weeks of cessation of molt and shortly following an upturn in body weight. In the other two birds the prenuptial molt was very incomplete, a few new replacement feathers appearing in middle to late March and early April. However, both lost weight during this time, approximately to the same extent as the birds described above. In both, the beginning of nocturnal restlessness occurred more or less coincidentally with an upturn in body weight.

In view of the varied previous history of these four birds, it should be mentioned that of the two "autumn captures" one went through an essentially complete molt resulting in typical cock plumage, the other remained essentially henney in appearance. Restlessness developed earliest (March 19/20) in the

male caught in the previous spring; it set in only three days later (March 23/24) in the "2nd year experimental" and in one of the two "autumn captures."

During this same winter, activity records were being obtained for a number of bobolinks caged indoors where night air temperatures never fell below about 11° C. Some of these birds were persistently active at night during December, when the outdoor birds had practically given up all exercise. In January an exchange was made, transferring an exceptionally active female to the outdoor aviary in place of one of the males, and putting him into her cage in the laboratory attic. The change in photoperiod was slight, from a constant 10 hours light-14 hours dark in the attic to approximately 11 hours light-13 hours dark in the

TABLE II

*Apparent effect of ambient temperatures on the nocturnal activity of two bobolinks, in an outdoor aviary (natural photoperiods, Lat. 36° N., outdoor temperatures) and in the laboratory attic (constant 10-hour photoperiod, 14 hours darkness daily, night temperatures from about 11° C. to about 17° C.). Activity Indices as in Table I.*

Periods	Outside temp. ° C.		Nocturnal Activity Indices					
	Aver. H	Aver. L	♂81			♀68		
			A	B	C	A	B	C
Dec. 27-Jan. 7	14	-1	0	0	0	34.7	59.0	2047
Jan. 3-8	8	-1	2	<1	2	26.3	54.1	1423
9-15	15	+3	0	0	0	6.9	5.0	35
16-23	12	0	32.1	71.2	2286	3.0	4.8	14
24-29	7	-6	27.9	89.2	2489	2.8	5.0	14
Jan. 30-Feb. 3	9	+2	4.6	56.3	259	5.0	5.0	25
Feb. 4-10	11	-2	42.3	141.2	5973	3.9	3.0	12
11-17	11	-1	3.4	6.2	21	24.6	60.9	1498
18-24	4	-3	0	0	0	30.0	64.6	1938

aviary. But there was a complete, almost dramatic reversal in the nocturnal activity performances of the two birds as they were shifted back and forth between the warmer and colder environments (Table II). Looking at these data, it is impossible not to suspect that temperature here is playing a decisive role in regulating the extent and degree of nocturnal activity.

In view of the subsequent development of nocturnal restlessness in the aviary birds (Table I) while night air temperatures were still regularly dropping below the freezing point, it seemed logical to test the hypothesis that this activity had been photoperiodically induced by exposing some birds at low air temperatures to long, others to short photoperiods. If warmer temperatures promote nocturnal activity in these birds when caged, and colder temperatures inhibit or suppress it, could a photoperiodic response "break through" and express itself as persistent perch-hopping during the night despite low air temperature? In the absence of suitable low-temperature control facilities, it was decided to make use of normal

winter temperatures and to repeat the outdoor aviary experiments, suitably modified, in the following year.

*Experiment 2 (Table III, Figures 1 and 2)*

In 1960-61 two aviaries were used and records of activity obtained for six males, three in each aviary. The aviaries were illuminated only by natural light until November 27. After this date one aviary continued to receive only natural light, while in the other white fluorescent lights (minimum intensity about 35 foot-

TABLE III

*Summary of nocturnal activity of two groups of bobolinks (3 ♂♂ each) in relation to season, natural and lengthened photoperiods, and ambient temperature, as measured by recorded perch-hopping movements January 3 to May 2, 1961, Chapel Hill, N. C., Lat. 36° N.*

Week ending	Air T ° C.		Nocturnal Activity Indices					
	Aver. H	Aver. L	Group AvN			Group AvL		
			A	B	C	A	B	C
Jan. 10	11	-5	2.9	9.1	26	1.1	1.6	2
17	12	-2	2.1	3.1	7	1.3	11.2	15
24	7	-6	2.7	2.7	7	1.0	1.3	1
31	3	-9	1.4	1.8	3	<1	2.0	<1
Feb. 7	6	-7	3.5	11.9	42	1.0	3.7	4
14	11	-2	4.6	5.5	25	1.2	8.8	11
21	19	+4	6.6	9.6	63	8.6	25.9	223
28	18	3	2.8	10.2	29	11.5	19.6	225
Mar. 7	20	7	7.7	20.7	159	19.0	35.4	673
14	19	5	8.4	19.7	165	16.5	40.9	675
21	15	1	10.6	18.3	194	18.8	41.0	771
28	14	1	25.3	27.9	706	26.1	50.1	1308
Apr. 4	18	4	29.3	37.4	1096	25.0	46.5	1163
11	16	2	27.8	38.1	1059	24.3	37.1	1273
18	18	4	17.6	30.1	530	22.9	38.5	882
25	21	8	31.0	45.9	1423	24.5	43.4	1066
May 2	22	9	31.1	38.3	1191	16.5*	35.2*	581*

Group AvN, outdoor aviary, natural illumination only; Group AvL, outdoor aviary, extra, artificial lighting, in addition to natural light, 5:15 A.M. to 7:15 P.M. daily from November 28 to April 20. Activity Indices as in Table I.

\* One bird apparently becoming inactive at night this week; no later records.

candles at perch level) burned daily from 5:15 AM to 7:15 PM. The constant artificial photoperiod was thus 14 hours, which previously had been shown to be stimulatory in the testicular photoperiodic response of bobolinks when preceded by several weeks of shorter photoperiods (Engels, 1961). In the naturally lighted aviary the photoperiods declined to about 10½ hours at the December solstice, then gradually increased but did not reach 14 hours until mid-April.

None of the bobolinks used was newly captured. However, two of the three birds in each group were in their second year in the aviary under continuously natural day-lengths, and of these, one in each group had never been exposed to artificial photoperiods.

The results are given in Table III. The winter was much more mild than the previous one, the weekly average low air temperatures remaining above freezing after mid-February, whereas in 1960 they remained below freezing throughout March. Nevertheless, a marked rise in the nocturnal activity indices for the naturally lighted birds (Group AvN) occurred in the same week, the last week in March, as it had for the aviary birds in the preceding year (*cf.* Table I). On the other hand, in the aviary birds exposed to 14-hour photoperiods this pronounced increase in nocturnal activity occurred about three weeks earlier.

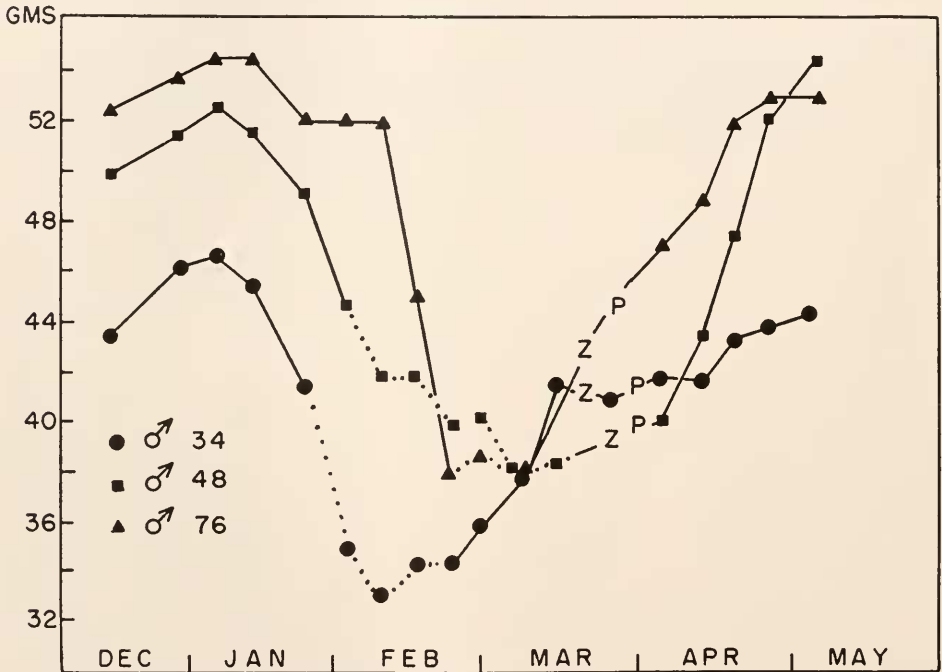


FIGURE 1. Variation in body weight of 3 male bobolinks in an outdoor aviary, Lat. 36° N., natural photoperiods; group AvN of Table III. Dotted lines indicate periods of molt; P: approximate time of beginning of nuptial pigmentation in the beak indicative of testicular recrudescence; Z: approximate time of onset of pronounced nocturnal restlessness. Body weights determined (usually) at one-week intervals.

This appears to be a definite acceleration of the cycle, which may be attributed to the lengthened photoperiod. Considering the long period of exposure to long days, about three months, before the response occurred, the acceleration seems slight indeed. Yet this result might have been anticipated from our previous studies on the testicular cycle of bobolinks, which demonstrated a long delay in the testicular response to photoperiodic stimulation (Engels, 1961, pp. 144-145).

The lean weight of male bobolinks is 30 grams or less. Birds weighing 40 grams or more are conspicuously fat, especially over the rump and in the abdominal region. As shown in Figures 1 and 2, all of the birds were very heavy through December and early January. All but one experienced sharp

losses in body weight between the end of January and the middle of February. Each of these also went through an almost complete prenuptial molt to the cock plumage. This molt did not occur in the single bird in which body weight remained high (no. 30, Fig. 2). The five birds which had lost weight, and which had molted, developed nocturnal restlessness subsequent to the molt and either just prior to or shortly after the beginning of increase in body weight. In all cases but one, the onset of nocturnal restlessness preceded the development of

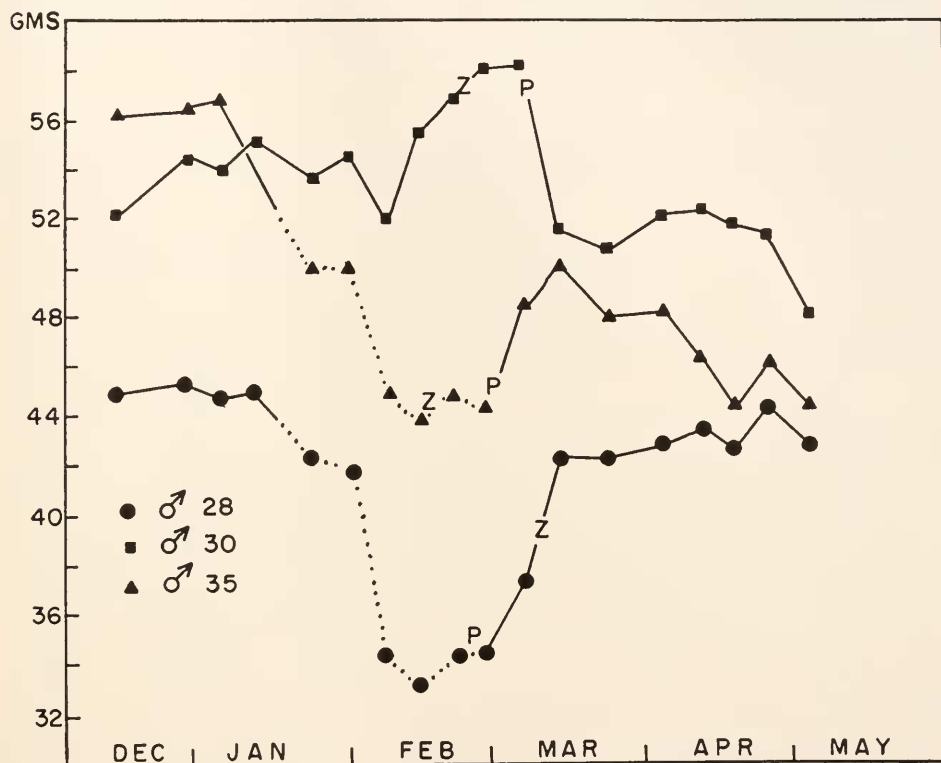


FIGURE 2. Variation in body weight of 3 male bobolinks in an outdoor aviary, as in Figure 1, but exposed to 14-hour photoperiods (5:15 A.M. to 7:15 P.M.) daily, beginning November 28; group AvL of Table III. (See also legend of Figure 1.)

beak pigmentation, as in the four aviary birds of the previous year, described above. One male (no. 28, Fig. 2) did not develop nocturnal restlessness until about 10 days after the beginning of peak pigmentation.

### Experiment 3 (Table IV)

This was essentially a duplication of part of the second experiment, using only "spring captures." Three males captured in the spring of 1961 were confined in an outdoor aviary. Beginning November 15, 1961, a 14-hour photoperiod (5:15 AM.-7:15 PM) was superimposed on the natural day-length



(white fluorescent lights; minimum intensity at perch level about 35 f.c.). A single perch in each cage was balanced on the tip of the 6-inch actuating arm of a microswitch. Perch-hopping activity was relatively infrequent at night until after the middle of March when restlessness became pronounced. There again appeared to be some correlation with ambient temperature, with flurries of restlessness, appearing during the weeks ending January 28 and February 25, associated with rises of air temperature. Throughout the period of recording, it was only when the weekly average of the daily mean air temperature exceeded 9° C. that the average index A was above 16 (= 4 hours), index B above 15 (= 1 hop per minute), and index C above 400 (hops per bird per night).

TABLE IV

*Nocturnal activity of 3 male bobolinks in an outdoor aviary at Chapel Hill, N. C., Jan. 7-Apr. 22, 1962; 14-hour photoperiod (5:15 A.M.-7:15 P.M.) superimposed on natural day-lengths beginning Nov. 15, 1961*

Week ending	Air T ° C. average			Nocturnal Activity Indices		
	H	m	L	A	B	C
Jan. 14	3	-3	-9	3.2	10.0	32
21	7	1	-5	6.3	7.4	47
28	16	10	+3	9.8	22.6	221
Feb. 4	9	3	-4	2.1	9.0	19
11	10	3	-3	4.5	6.3	28
18	9	3	-3	2.7	11.7	30
25	16	10	+4	6.9	39.7	274
Mar. 4	11	6	+1	8.4	11.5	97
11	6	2	-1	1.8	3.7	7
18	13	7	+1	12.5	10.8	135
25	17	10	3	22.6	19.1	432
Apr. 1	20	13	6	19.0	27.3	519
8	18	12	5	20.2	27.0	545
15	19	14	8	20.7	18.3	379
22	24	15	5	18.3	24.2	443

One bird developed the black pigmentation of the beak characteristic of testicular recrudescence during the week ending February 28. The same bird abruptly became restless at night about two weeks later on March 11/12. The other two males both developed black pigment in the beak during the week ending March 8 and a very distinct beginning of heightened restlessness on the night of March 18/19.

#### DISCUSSION

The primary question is: "Does pronounced nocturnal restlessness in these caged bobolinks reflect a disposition to migrate?" Questions as to the induction and regulation of the restlessness must remain secondary, and academic, until the first is answered. The results of the present experiments are not unequivocal.

The relatively abrupt change in nocturnal behavior in all experiments occurred during March. Northward migration of free-living birds probably begins in the

latter part of March and early April. (The first flocks of migrating males usually arrive in the coastal areas of the southernmost U. S. shortly after the middle of April. I have seen three male specimens taken between Lat. 22° S. and 17° S., within the "wintering" area, on March 23, 28 and April 1.) Had the experiments taken place in South America, the near coincidence of the onset of restlessness with the migratory season might be interpreted as meaningful.

There was also some degree of correlation between the onset of pronounced nocturnal restlessness and some other cyclic events which are associated with migration, namely molt, fattening, and testicular recrudescence. *None* of the several museum specimens I have seen from the "wintering" grounds has the black beak indicative of testicular recrudescence, even though three were collected (between Lat. 22° S. and 17° S.) as late as the last week of March. Moreover, thirteen South American April specimens definitely were migrants, and of these, nine (northern Brazil, Venezuela) likewise had light-colored beaks. In the other four (Colombia) the beak was darkening at the time (collector's hand-written notes on labels indicated color of "mandible" as "gray," "light gray," and [two] "gray with border and point black," respectively).<sup>3</sup> Evidently migration gets underway before the blackening of the beak. In our experiments, pronounced nocturnal restlessness set in after the change in beak pigmentation in only four of thirteen cases, in another one the two events occurred more or less simultaneously, while in eight the onset of restlessness occurred before the change in beak pigmentation, just as in nature the beginning of migration precedes this event.

A molt from the winter "henmy" plumage to the nuptial "cock" plumage may be complete by the end of January (University of Michigan #90875) but apparently more usually occurs during February and March. At any rate it is completed before northward migration begins. Presumably premigratory fattening occurs subsequent to the molt, but I have no information about this. (Datum on weight is given on the label of only one of almost 100 museum specimens, known to me, taken south of the U. S. Spring migrants taken in the southern U. S. are conspicuously fat.)

Our caged birds tended to remain fat throughout the year, except during periods of molt. Molt in these birds presents a puzzling problem. In some the molt to nuptial or "cock" plumage was essentially complete, in some it was partial, in some it was more or less completely suppressed. These differences appeared among birds with identical previous history of capture and treatment. However, when molt was complete (or partial), it occurred prior both to the onset of pronounced nocturnal restlessness and to the development of black beak pigmentation. Following the molt there was always a sharp rise in body weight, caused by the deposition of fat. The onset of pronounced nocturnal restlessness was always associated with this rise in body weight.

All of these observations, associating nocturnal restlessness with season, fattening, molt, and testicular recrudescence in a general temporal sequence comparable to that obtaining in nature, at least suggest that the restlessness of the caged birds reflects a true migratory unrest. Since there is no good reason to suppose that these

<sup>3</sup> Grateful acknowledgment is here made to the following for the loan of specimens: Dean Amadon (American Museum of Natural History); Kenneth C. Parkes (Carnegie Museum); Emmet R. Blake (Chicago Natural History Museum); Harrison B. Tordoff (Museum of Zoology, University of Michigan); James Bond (Philadelphia Academy of Sciences); P. S. Humphrey and Mary A. Heimerdinger (Peabody Museum of Natural History).

various events are all causally related, the few discrepancies in sequence in the experimental birds are not unexpected. The mechanisms responsible for each may proceed from different thresholds, from different stimuli, at different times and along different pathways, the natural coordination of which may be upset by the experimental treatment. One may surmise, for example, the existence of an antagonism such that if the hypothalamic-hypophyseal gonadotropic mechanism gets started a bit relatively early in a particular captive individual, the mechanism(s) leading to molt may be partially or fully inhibited.

In studies on temperate-zone migrants, the experimental birds are obtained on the wintering grounds, after the fall migration has been completed. Our bobolinks were caught in May and in September, and hence their southward migration was prohibited. That a nocturnal restlessness tended to persist in them is not surprising since it is a common observation that caged birds under natural photoperiods remain in a state of migratory unrest far beyond the natural migratory period, often until the next molt (*cf.* Farner, 1960). The restlessness in our bobolinks caged out of doors was inhibited seemingly by low environmental temperatures (*cf.* Table II). Nevertheless (in Experiment 1, Table I) pronounced restlessness set in, during March, when air temperatures were still below freezing every night and the daily mean temperature averaged only about 5° C. As Schildmacher (1938) concluded from rather comparable observations on European robins (*Erithacus rubecula*), “. . . one must assume that in these birds the effect of [an inductive mechanism] overweighed the effect of low temperature” (p. 151, free translation).

In the quoted statement Schildmacher actually specified “lengthened daylight” as the inductor. That lengthened daylight may play a role in the development of nocturnal unrest in bobolinks is indicated by the results of our Experiment 2 which show that this activity appeared earlier in birds exposed to 14-hour photoperiods as compared to those experiencing only natural (winter) photoperiods (Table III). Farner (1960) has reported positive results in similar experiments with *Zonotrichia leucophrys gambelii*; a chief difference in the data lies in the lapse of time between the first 14-hour photoperiod and the *Zugunruhe* response—a few weeks for *Z. l. gambelii* (a temperate-zone migrant), more than three months for bobolinks. A similar delay appears in the photoperiodic induction of testicular development in bobolinks (Engels, 1961; also Fig. 2, above); it seems to be an essential part of this species' adaptation to the long days it experiences in the southern hemisphere between breeding seasons.

A. J. Marshall, a notable and vigorous protagonist of the idea that photoperiod is concerned with reproduction of birds only insofar as it may influence an internal rhythm, has stated (Marshall, 1961, p. 331) that “Spring *Zugunruhe* is a behavior pattern that is undeniably activated by photostimulation and probably by testosterone.” If genuine migratory unrest in bobolinks is in any way activated by testosterone, either the testosterone must be stimulatory at a threshold concentration far below that which produces a change in pigmentation of the beak in the male or the behavior response must occur much more quickly, since, on the evidence of museum specimens, bobolinks in their northward migration may reach northern South America without showing this change. Doubt is cast on any testosterone activation by those experimental cases in which the beak became black as much as two weeks before the onset of pronounced nocturnal restlessness (Experiment 3).

It should be admitted that, from the evidence obtained thus far, the possibility is not precluded that annual cycles in this transequatorial migrant may rest fundamentally on an internal rhythm as "the primary seasonal initiator" (Marshall, 1961, p. 309). Actually, the very long delay in response to 14-hour photoperiods, the slight acceleration as compared to natural (winter) photoperiods (Experiment 2), might readily be interpreted in terms of this concept.

#### SUMMARY

1. The bobolink (*Dolichonyx oryzivorus*) is a transequatorial migrant which breeds (June-July) above Lat. 40° N. in North America and "winters" (November through March) below about Lat. 10° S. in South America. The northward migration occurs during April and May.

2. Observations on nocturnal restlessness, molt, body weight and the testicular cycle were made on some captive bobolinks at Lat. 36° N., caged out-of-doors and exposed to natural as well as to lengthened photoperiods, and to normal outdoor air temperatures. "Restlessness" was recorded every quarter-hour, by an electronic counting device, as the number of hops made by each bird on the perches of its cage.

3. Restlessness was almost completely suppressed by the low air temperatures of winter. Nevertheless, intense nocturnal unrest set in rather abruptly in late March when air temperatures at night were still regularly below the freezing point (natural photoperiods).

4. When 14-hour photoperiods were superimposed on natural day-lengths, beginning November 28, restlessness set in about three weeks earlier than in the controls which experienced only natural day-lengths. This was interpreted as evidence at least of a photoperiodic influence on, if not photoperiodic induction of, nocturnal restlessness.

5. The onset of pronounced unrest was always associated with a marked rise in body weight, due to the deposition of subcutaneous and intraperitoneal fat, usually following a molt. In most cases this onset of restlessness preceded, by an appreciable interval, the appearance of black beak pigmentation, which indicates testicular recrudescence. These temporal relationships correspond to a sequence of events in nature and are tentatively interpreted to mean that the restlessness reflects the induction of a migratory state.

6. The long delay (about three months) in the response to the presumed stimulation by long photoperiods is similar to the delay found in the response of the testicular cycle to photostimulation. An interpretation in terms of an internal rhythm as a primary seasonal initiator, with other factors (such as photoperiod) acting as accelerators-inhibitors, is not precluded.

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